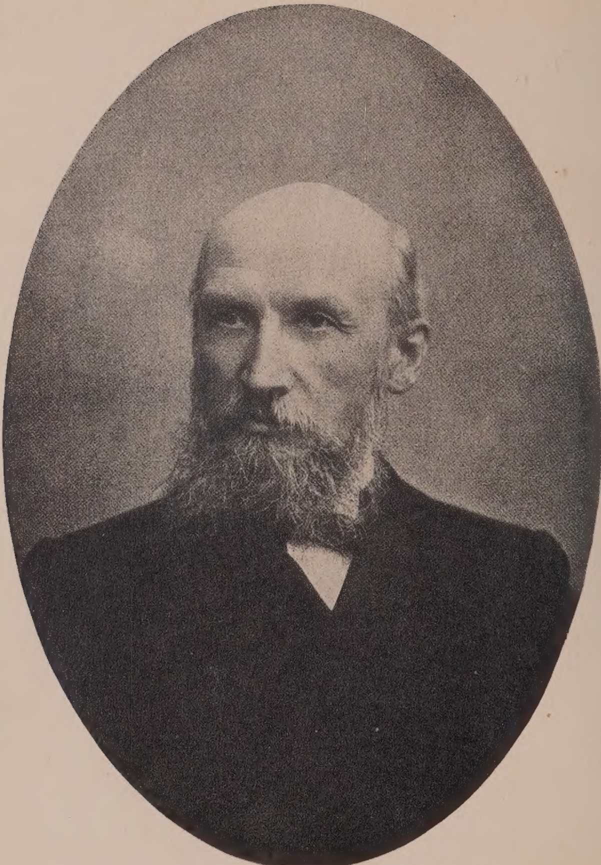

Dr M. Woronin.
born at St. Petersburg
21 July / 2 August 1838.

photog. 1900.

Phytopathological Classics

NUMBER 4

PLASMODIOPHORA BRASSICAE

THE CAUSE OF CABBAGE HERNIA

By

MICHAEL STEPHANOVITCH WORONIN

1878

A Translation
from the German by
CHARLES CHUPP

With a Biographical Sketch
by the Translator

Published by the
AMERICAN PHYTOPATHOLOGICAL SOCIETY
1934

ACKNOWLEDGMENTS

THE chief source of inspiration in the preparation of this publication has been Professor H. H. Whetzel. His original suggestion that the translation of Woronin's classical paper on club root be undertaken and his kindly prodding has from time to time revived our flagging spirit at critical moments.

To Dr. Wm. H. Weston of Harvard University we are indebted for the loan of Woronin's original article in Russian, published privately in St. Petersburg in 1877 and of which the well known German publication is an exact translation.

We wish to acknowledge our indebtedness to Miss Vera G. Turin, student at Cornell University, for her exceptionally well done translation from the Russian of the obituary of Woronin by Famintzin, which has served as the chief source of data in our preparation of the biographical sketch.

C. C.

MICHAEL STEPANOVITCH WORONIN

Michael Woronin was fortunate in a number of ways, which no doubt enhanced his success in science. He was well educated by a wealthy father, he had enough money of his own, so that he did not have to waste time in striving for a living, and had no family on which to lavish time and effort. Therefore, he was free to follow his investigations with undivided attention. He even had a laboratory in his bed room so that he did not need to waste time in going to or from his work.

But all the favorable surroundings imaginable can not make a successful man unless he has the ability to take advantage of every opportunity. Even though Woronin's brothers were given the same training as he, they never became renowned research men. Probably Michael, even when very young, had that infinite patience and deep sense of correct interpretation that later caused his work to be done so carefully that its scientific significance will endure as long as does the science of Phytopathology.

Michael Woronin (Voronin, in the Russian) was born in St. Petersburg July 21, 1838. His father spared no expense in giving him and his brothers the best training possible. His tutor was a German, who must have left a deep impression on the youth, who, through his entire life, cherished a well-known sympathy for Germany, its language, literature, and customs. At the age of sixteen Woronin entered the University of St. Petersburg where he studied natural history and especially geology. When he graduated in 1858 his thesis on granite and diorite rocks was so outstanding that he was presented with a silver medal.

After the commencement, he immediately went to Germany in company with his classmate Famintzin, to whom we are indebted for almost all the biographical material on Woronin now extant. It is true that Nawaschin, also a Russian and a coworker, wrote a very flowery eulogy of his friend, but contributed very little to our knowledge of the actual facts of his life.

Woronin spent two years abroad studying botany, at first in Heidelberg under Holle, and later in Freiburg in the then unassuming laboratory of Anton de Bary. De Bary's presentation must have been very impressive to young Woronin who became his teacher's close friend and correspondent and who modelled his methods of research after those of this great master. Not only that but he finally gave up all other botanical subjects in favor of mycology, especially the development and life histories of fungi, a subject then being made so interesting by the investigations in de Bary's laboratory at Freiburg. Notwithstanding his later inclinations, his first work under de Bary was the preparation of a paper on the stem anatomy of Calycanthus.

During the summer of 1860 he worked on sea algae in the Gulf of Genoa and later wrote an article on *Acetabularia* and *Espera*. This paper served as a thesis for his Master's Degree in Botany which he received from the University of St. Petersburg in 1861. This was his first and last endeavor in the procuring of a degree.

During the next dozen years, he worked so assiduously and published such clearly stated and beautifully illustrated pieces of research, that he began to be well-known in all botanical circles, and organizations felt proud to do him honor. The new University of Odessa in 1874 gave him an honorary degree of Doctor of Botany. He was invited to membership in several Naturalists' societies, the Russian Olericultural Society, German Botanical Society, the Linnean Society of London, and he was made an honorary faculty member of the Royal Universities at Dorpat and Kharkow.

Woronin apparently was jealous of his time for study, and took part in very few outside activities. He was a private docent in the University of St. Petersburg from 1869 to 1870 where he lectured on mycology. From 1873 to 1875 he lectured on mycology and on the morphology of the cell at a medical school for women. His one hobby seemed to be the secretaryship of the botanical section of the Natural Science Society of St. Petersburg. He served faithfully in this position for thirty years. It gave him an opportunity to review all the new botanical literature and keep in touch with workers throughout the entire world.

A man in so prominent a position naturally was called upon to solve a number of immediate problems in phytopathology. His kindliness of spirit never permitted him to refuse such help as he could give, even though it took him away from his favorite group of fungi, the Sclerotiniæ. To this category of work may be referred his paper on "intoxicating bread," in the South-Ussurian Region. Bread made out of certain rye flour caused, headache, dizziness, and vomiting. Woronin with his usual thoroughness found that fifteen different fungi were associated with the grains of rye and that four of these were the most dangerous ones in producing the ill effects when taken within the human body. For some reason or other, he was at one time requested to study the flora of the large intestines, a report of which he made to his society later. Another problem was the sunflower rust, which was driving peasants out of the sunflower industry. Woronin not only worked out the life history of the fungus, but in his final publication suggested a number of practical control measures.

Probably his greatest contribution to the pressing plant-disease problems of his time was undertaken not through a direct request by the people, but because he wished to aid the market gardeners in the vicinity of St. Petersburg. This was his classic investigation dealing with the club-root of cabbage. This work was done so carefully and recorded so accurately that, although many papers have been written since on the subject, little has been added to that originally observed by him.

No doubt a bedroom laboratory in St. Petersburg would pall upon even the most monkish type of investigator if the monotony were not broken by outside activities. At least Woronin found it desirable to make fairly frequent trips to Germany where he applied himself, either alone or in co-operation with some other worker, to various types of investigations. But, apparently, by far the most pleasant outings were his summer trips to his villa in Finland. Here he entertained his friends by taking them to the cool bogs nearby where representatives of many genera of the heath family grew luxuriantly and where Sclerotiniae were present in great abundance. Studies on the life history of these forms then took the place of recreation in his life. He was never too busy to discuss any phase that might be concerned

with these cup fungi. Naturally, the investigation finally widened to include the monilioid forms causing brown rot of cultivated fruit.

The subjects that have been mentioned do not nearly complete the record of Woronin's research activities. Famintzin concludes his biography with a citation of sixty-four papers published by Woronin. Nawaschin also included the same list in his tribute to the author.

A man of Woronin's wealth must often have been solicited for financial help. At least it is known that he willingly aided in several educational causes. Among these were donations to the University of St. Petersburg for the building of the Botanical Institute and for the establishment of a Biological Station at Bologoé. He made it possible to publish a review of the scientific activities of the Botanical Section of the Natural Science Society of St. Petersburg for a period of twenty-five years from the time of its foundation. Furthermore, he usually paid for the insertion of his own well-drawn illustrations (frequently colored) and in this way was of direct service to the publications in which his articles appeared.

According to his two biographers, Woronin was ever kindly disposed toward the people he met. He was studiously careful not to hurt the feelings of any one. He was liberal in time and money. He was painfully modest and abhorred argumentation. All these attributes endeared him not only to his fellow workers but also to the average man about town, so that he was mourned by a large circle of friends when he died February 20, 1903.

—Charles Chupp

Famintzin, A. S. Obituary of M. S. Woronin. Report of the St. Petersburg Imperial Society of Naturalists **34**:1-13. 1903. (Same article reprinted in Travaux du Musée Botanique de l'Académie Impériale des Sciences de St. Petersburg **2**:1-13. 1905). This article has been translated into English by Vera G. Turin. Copies of this are available in the Library of the Plant Pathology Department of Cornell University.

Nawaschin, S. Michael Woronin. Berichte der Deutsche Botanische Gesellschaft (Generalversammlungs Heft). **21**:(35)-(47). 1903.

PLASMODIOPHORA BRASSICAE THE CAUSE OF CABBAGE HERNIA*

by M. Woronin

During recent years the "hernia" of cabbage plants has become very widespread and at the present time is causing serious losses to the vegetable gardeners in many Russian communities, especially in the environs of St. Petersburg. The cause of this disease and the methods for its control have remained unknown until now; consequently, the Royal Russian Gardening Society (in St. Petersburg) in 1872 posted a prize for a scientific investigation on the subject. The latest date on which such a work could be handed in was set as November 1, 1873. When at the termination of this period nothing had been offered, the date was advanced two years, that is, until November 1, 1875; and when the second announcement remained without results the date again was extended two years, or until November 1, 1877.

For my part, I undertook the investigation of the cabbage hernia quite accidentally and wholly independent of the announcement by the committee. I began the work in 1873 and did not complete it until the autumn of last year (1876); thus the discussion that I present here is the result of three years' work. I succeeded in discovering that the actual cause of the disease is a new organism, which I have named *Plasmodiophora brassicae*. I investigated its life history as thoroughly as possible and by means of cultural experiments proved to myself that this organism is the only cause of cabbage hernia. After I was sure of the pathogen, it was not difficult to turn to control measures, which, though not completely eliminating the disease, might appreciably decrease its development.

* (Translator's Note:—Although this translation has been made from the German edition published in the *Jahrbücher für wissenschaftliche Botanik* Vol. XI, a careful comparison with the original Russian edition published privately in 1877 under the same title shows the German to be an exact translation. M. Woronin's first publication on club root was: Die Wurzelgeschwulst der Kohlpflanzen, Botanische Zeitung **33**:337-339. 1875. This is a summary of his talk before the Botanical Section of the St. Petersburg Naturalist's Society, March 5, 1874).

I made a preliminary report of my investigations to the Botanical Division of the St. Petersburg Natural Science Society, February, 1874[1]; later to the fifth gathering of the Russian Natural Science Society in Warsaw; and to the Botanical section of the St. Petersburg Natural Science Society, November 18, 1876.

I obtained the materials for my investigations, that is, cabbage plants affected with hernia, in St. Petersburg and its immediate vicinity (among others, also in the village of Vira in the Zarskoie-Selo district) as well as in the region of Wiborg (in Finland).

I take the opportunity here to express my deepest appreciation to those who came to my aid with their cooperation, either in providing needed materials or by drawing my attention to several statements in literature.

I extend especial thanks to Messrs. P. Wolkenstein, E. Regel, E. Gratscheff, N. Kniper, E. Junge, C. Gernet, C. Maksimowitsch, A. Batalin, E. Ender, A. Hackmann, and Mrs. P. Tarnowsky.

I

The disease of cabbage, known generally by the Russian vegetable gardeners under the name of crucifer hernia (Kapoustnaja kila), is portrayed by characteristic swellings of various shapes and sizes on the roots of affected plants. The disease rarely is confined to a very few swellings on a limited number of roots, and in such cases the plant suffers no injury, or at least none that is noticeable. Much oftener the swellings appear in great numbers and in such masses that all the roots are covered. The crowded roots of such diseased cabbage plants, being entirely disfigured, have a wholly different appearance from those of the healthy plant. Such an extreme development of the root hernia produces on the cabbage plant a very pronounced injury, which is made evident on the part of the plant above ground either by the total absence of a head or of one that is much retarded in its development.

It is possible to find cabbage plants with well-developed heads and yet have roots that are partly or wholly covered

[1] This report has been made available also in the German language. (Bot. Zeitung, 1875, p. 337).

with the hernia swellings. Such cases occur if the infection takes place when the cabbage plant is well-grown rather than when it is very young. This shows that the plant is susceptible in all stages of development, and, in fact, hernia can be found on cabbage from early spring, while it is still a seedling in the hot bed, until late autumn, after the heads have been cut from the stalks.

The form of these heterogeneous crooked swellings of the root—these hernia excrescences—usually is so variable and irregular that it is very difficult, yes, even impossible, to give a suitable and correct description of them. I therefore refer to figures 1-5 (Plate 29) and figures 6-11 (Plate 30), in which the cabbage hernia is illustrated in natural size and in its most variable stages of development.

The size of these most abnormal and, for the most part, formless root protuberances is quite variable, as may be judged from the illustrations. The most remarkable excrescences I had the opportunity to examine were the size of a healthy man's fist. Incidentally, it may be mentioned that the very largest hernia swellings are found mostly on the taproot; the swellings that occur on the secondary roots are, as a rule, much smaller.

The color of the hernia protuberances is the same as that of the healthy roots; namely a greasy-gray or pale yellow. In a cross section the excrescence is snow white and of a fairly firm texture, being as easily cut with a sharp knife as is a potato tuber or any turnip. This, however, is true of the hernia swellings only in the beginning; later they wrinkle, shrivel, and decay, take on a dark color, and finally become a rotten, decayed, almost liquid-like, dark brown mass, which usually emits a very strong foul odor. So far as I was able to observe, the hernia swellings in dry soil exist for a fairly long time without any visible change. On the other hand, in wet ground and especially after a heavy rain of several days they rot extremely rapidly. In the process of decay the parenchyma tissue of the root falls completely apart, while the vascular bundle retains for some time the form of fiber bundles. (Compare Plate 29, Fig. 2; Plate 30, Fig. 6). In most cases the decay begins at the lower part of the taproot and on the secondary roots that are deepest in the ground. While these lowest excrescences are decaying gradually, new

roots grow on the upper part and in turn also become diseased and covered with hernia swellings, after which the process is again repeated. Finally, new roots are put out from the base of the cabbage stem and even from the leaf scars on these stems. In vegetable gardens one can find such cabbage plants, which are fastened to the soil only by these upper roots, part of which are above ground, while all the remaining roots are not only diseased, but already appear half-decayed.

The hernia disease attacks all kinds of crucifers, the common cabbage (white, as well as red), cauliflower, borecole, savoy, kohlrabi, all cabbage and turnip varieties (*Brassica Rapa* and *Br. napus*), rape, etc., and not only all species of the genus Brassica, but also several other plants of the crucifer family; for instance, hernia is found on *Iberis umbellata* (Plate 30, Fig. 9) and on stock.

The hernia seems to be a general and widespread evil; at least, it is well known not only in Europe but also in America. It apparently is present in the whole of Europe. I, myself, have found it and investigated the disease in Russia (in the environs of St. Petersburg and Warschau) and in Finland (near Wiborg). Aside from this I have a long list of accounts, both private and in literature regarding the presence of this disease in England, Scotland, Belgium, France, Germany, and Spain. In England hernia is known as Clubbing, Club-root, Ambury, Anbury or Hanbury, or also as Finger-and-toes.[2] It is well known by the last name also in Scotland and America. The Belgians name it "Vingerziekte" or "maladie digitoire." In Germany the hernia goes by the name of "Kelch or Kropf des Kohles." It is found in many localities in Germany; for instance, in the environs of Hamburg, along the Rhine, in the Harz Mountains, in Würzburg, and in Prussia (in Gumbinnen).[3] The Spaniard, Ruiz Diaz de Isla, one of the oldest syphilographers, says that in his country syphilitic swellings occur

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[2] Compare Gardener's Assistant, p. 245 and 361; Charles Mintosch: The Book of the Garden, **1**:111; Johnson: The Cottage Gardener's Dictionary p. 28.

[3] I obtained these data from *Hamburger Garten- und Blumenzeitung* by Ed. Otto (vol. 9) Hamburg 1853, **1**:433, 477, 514, and 535; and from *Zeitschrift des Landwirthschaftl. Vereins für Rheinpreussen,* (No. 5, vol. of 1853). Regarding the appearance of hernia in Prussia (*in Gumbinnen*) compare R. Caspary: Eine Wruke (*Brassica napus* L.) mit Laubsprossen auf knolligern Wurzelausschlag in the *Schriften d. Physik.—Oekon. Gesellschaft zu Köningsberg* vol. of 1873, p. 109.

on cabbage plants. From his description, the swellings are undoubtedly nothing more than cabbage hernia.[4]

Although hernia is so generally distributed, an investigation of the disease has been wholly neglected, even to the present day. In recent years it has developed most rapidly in Russia,—a phenomenon very easy to explain. In no other country is cabbage grown so intensively as in Russia. According to an estimate made by Mr. E. Gratscheff (one of the most prominent vegetable gardeners of St. Petersburg) the annual income derived from cabbage growing in the St. Petersburg district alone amounts to the impressive sum of 300,000 rubles (about $153,000). The Russian truck gardeners suffered especially in the late 60's and early 70's so that, for example, in 1869, according to the statement of E. Gratscheff, half of the cabbage crop about St. Petersburg was destroyed by hernia. Such a severe attack by the disease naturally caused the vegetable growers a very considerable loss, so that finally they were forced to pay adequate attention to the appearance of the trouble. This gave rise to the Vegetable Gardener's Association of St. Petersburg, an organization for the inauguration of a scientific investigation of cabbage hernia.

If now we turn to literature, we do not find one work in which the hernia is subjected to a strictly scientific investigation. Because of this, it is conceivable why the true cause of the outbreak has remained wholly unexplained until the present day. Most of the land owners and gardeners who have studied the matter closely have come to the conclusion that the disease is produced by a whole series of insects, among the most important of which are the following forms: *Anthomyia brassicae*, *Anthomyia trimaculata*, *Curculio pleurostigma*, *Curculio contractus*, *Centorhynchus sulcicollis*, *Centorhynchus assimilis*.[5] This, however, is an error, the insects

[4] I give here the exact words of Ruiz de Isla, which I quote from Dr. E. Lancereaux's *Traité historique et pratique de la Syphilis* second edition, Paris, 1873 p. 591. Ruiz de Isla says as follows: "At Baiza in my own country, I have noticed cabbages attacked by syphilis. This disease is communicated to them by stagnant water in which the linen of syphilitic patients has been washed and which has been used afterward to water the plants. The swellings of these resemble the pustules of the disease to such a degree that the children cut them with shears and paste them on their faces to imitate the disease. Besides, also other vegetables, as well as a great number of animals, suffer from the malady."

[5] Compare Rob. Thompson: *Gardener's Assistant*, **1**:245 and 361; G. Johnson: *The Cottage Gardener's Dictionary* (1857), p. 28; C. Mintosch: The *Book of the Garden*, **2**:111; Boisduval: *Essai sur l'Entomologie horticole*, p. 145; Taschenberg's *Ento-*

being merely secondary. Usually no insects are found in fresh protuberances of hernia as long as they remain firm, but do appear in the swellings that have begun to decay—a thing that already has been observed in England.[6] The excrescences in their decay and disintegration play the same rôle for insects as do any other decomposing organic substances, such as meat, fruit, mushrooms, and the like. Here the insects lay their eggs and the larvae develop in the rotting mass. Similarly, the insects may be observed to follow the hernia and in no case are the cause of it. As early as 1872 Mr. A. Wehitschkoff (farmer and landlord of Gschatsch) remarked quite correctly that cabbage hernia was not caused by insects.[7]

So far as the botanists are concerned, not one of them has conducted a careful investigation of the disease. J. Kühn (*Die Krankheiten der Kulturgewächse*, 1858, pp. 252 and 253) differentiated two types of swellings on cabbage roots. According to him, the one was produced by *Anthomyia brassicae* and the other, J. Kühn likened to the swellings that occur on the trunks and branches of conifers (for example, *Pinus picea*) as well as those that appear on beets, and in whose development, as he says, no insects take part. The excrescences on cabbage plants were mentioned only briefly by P. Sorauer (*Handbuch der Pflanzenkrankheiten*, 1874, p. 167) who attributes them to *Ocyptera brassicaria* F.

The only and at the same time perfectly correct illustrations of hernia (on rape) are given by R. Caspary.[8] Although he made a microscopical-anatomical study of the protuberances, he was not fortunate enough to discover the real cause

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mologie in the Russian translation by Baillon (1871).—In the *Berichte des Schulactes der Petrowsky-Rasoumowsky 'schen Landwirtschaft- und Forst-Akademie in Moskau* for the year 1873 it says on page 33: "The cabbage and turnip plants were heavily infested by three species of cabbage flies (Anthomyia). The roots of such plants were seriously injured by these insects and were covered with swellings which disappear in decay." In one of the *Sitzungen der Kaiserl. Russischen-Gartenbaugesellschaft in Petersburg* (for Jan. 15, 1872) Mr. Iversen declared that he had investigated the cabbage hernia collected in Mr. Gratscheff's gardens and hoped that by spring (1873) he would be able to identify the insects. He was of the opinion then that not only a Coleopter but a Dipter was involved.

[6] Compare the English literature cited in the previous foot note.

[7] Compare "*Die Berichte der Kaiserl. Gartenbaugesellschaft zu St. Petersburg,*" 1872, p. 440 (in Russian).

[8] R. Caspary: "Eine Wruke (*Brassica Napus* L.) mit Laubsprossen auf knolligerm Wurzelausschlag" in *Schriften der Physik-Oekon. Gesellschaft zur Königsberg*, 1873, p. 109; Plate XIV, Fig. 1-3—"Hereditary Deformity in *Brasscia napus*" in the *Gardener's Chronicle*, **3**:148, Fig. 25, Feb. 1877.

of their origin. He found, he says, "No sign of fungous hyphae or insect stings or any other exterior injury that presumably could produce such nodules."

R. Caspary paid less attention to the excrescences themselves than he did to the leaf buds that arise from them. I often observed such leaf buds on the root swellings of hernia not only on rape but also on common cabbage (Plate 30, Fig. 6), and especially did they develop luxuriantly on kohlrabi. The appearance of leaf buds on the root excrescences of hernia is of itself a most interesting phenomenon, which, so far as I know, never occurs on healthy roots and appears only on diseased cabbage roots that are deformed by hernia.

The real cause of hernia remained unknown up to the present day, and I was fortunate enough to unravel the mystery while investigating the swellings on diseased roots. I found a new organism, which I have named *Plasmodiophora brassicae*. It dawned upon me gradually from my study of its life history that it must be regarded as the only cause of cabbage hernia.

R. Caspary published a short note in the *Gardener's Chronicle* (February of this year) in which he announced the results he obtained when he sowed the seed of diseased rape. He considered the appearance of the heterogeneous nodular swellings on the rape and the development of leaf buds on the abnormal roots as a natural, constant phenomenon. In his opinion, they were reproduced inheritably through the seed. Undoubtedly this assertion is false.*

The results announced by R. Caspary can be explained very simply as follows: he planted the seedlings which he grew from the seed of diseased rape in soil in which without doubt spores of Plasmodiophora were present; and in my opinion, the cause of the affected seedling was then due to these spores. So far as the leaf buds on the roots are concerned, they can develop into new individuals, as R. Caspary's own experimentation showed, and can even play the rôle of seedlings. I should give no one the advice, however,

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* Translator's Note: Woronin, M. Nachträgliche Notiz zur Frage der Kohlpflanzen-hernie, *Botanische Zeitung* 38:54-57. 1880. This was a correction of his previous opinion that all swellings on roots probably were caused by an organism like Plasmodiophora, and to notify the public that he was wrong in believing that Caspary's "Monstrositus" on *Brassica napus* was a form of hernia.

to employ them in this manner, for all these leaf buds are already affected with the disease; in other words, they already contain the Plasmodiophora (compare Fig. 45 of Plate 33).

II

Before I begin the description of Plasmodiophora, I should like to discuss briefly two not unimportant related topics.

1. In the spring young cabbage plants, while they are yet in the hot bed, often may die; but the cause of this is in no way related to the development of Plasmodiophora. The outer parenchymatous tissue of the hypocotyl of the young seedling, while still in the cotyledonous stage or at most bearing only 2-3 pairs of stem leaves, begins to decay at the joint. It usually takes place where the stem joins the root near the surface of the ground. The delicate stem of the young plant becomes limp, bends over until it lies on the ground, and then generally rots away. A microscopic examination has shown that this destruction of the young seedlings is caused by a Chytridium that penetrates the roots and the hypocotyl stem and there achieves its full development. I am proposing the name *Chyt. brassicae* for this new Chytridium. The structure and complete development of *Chyt. brassicae* is exactly like that of the other Chytridium species. The following species, however, are most closely related to it: *Chytridium (Olpidium) endogenum* Al. Br., *Chyt. apiculatum* Al. Br., *Chyt. saprolegniae*, Al. Br., (*Olpidiopsis saprolegniae* Cornu) and *Olpidiopsis incrassata* Cornu.[1] Because of the great similarity to the above named forms and aided by the illustrations in figures 12-18 (Pl. 31), the description can be given very briefly.

Each globose zoosporangium of *Chyt. brassicae*, as shown in the illustrations, possesses a slender neck, the length of which may vary greatly. The zoosporangia that cling in the epidermal cells of the hypocotyl joints or in the cells of the root epiblem have very short necks, while those in the deeper tissue, that is, the cortex, always are seen to have a much longer neck. It is not unusual to find such necks that had to

[1] Compare Al. Braun: Ueber Chytridium 1856, p. 61.—M. Cornu: Monographie des Saprolégniées. *Ann. des sc. nat. V. séries*, 15:145-146, pl. 3 and 4. 1872—N. Pringsheim: *Jahrb. für Wissenschaftl. Botanik II*. p. 219. Pl. XXIV.

break their way through 3 or 4 or even 5 layers of cells before they reached the surface of the host plant. This zoosporangial tube opens on the surface of the host to discharge the zoospores. I found many zoosporangia, however, that opened within the host and liberated the zoospores into the cells of the parenchyma, which sustained the fruit body.—The zoospores of *Chytridium brassicae* (Pl. 31, Fig. 15), are composed of a naked, globose, fairly uniform mass of protoplasm, which, as is true of all the swarmspores in the genus Chytridium, possesses a single cilium, and within the mass contains a small vacuole as well as a hyaline oil-drop-like nucleus mostly of very slight dimensions.

Aside from the zoosporangia, *Chytridium brassicae* possesses also other reproductive organs, namely the resting spores (resting cells, which are nonmotile). I found these in the epiblem cells of the roots (Plate 31, Figs. 16, 17, 18). They are colorless or faintly yellowish, have a proportionately thick membrane, and are more or less star-shaped which gives them a certain resemblance to the cysts of Amoebae or Infusoria. The protoplasmic content of these bodies is hyaline, finely granular, and usually provided with a larger or smaller oil-droplet. I was unable to follow either the development or the further fate of these bodies. According to analogy with similar resting spores found in other Chytridiaceae and lately carefully investigated by Cornu and Nowakowsky,[2] one may safely assume that the resting spores of *Chytridium brassicae*, like zygospores, originate through the fusion of two protoplasmic bodies and, after a definite period of rest, are transformed into zoosporangia.

2. I wish now to make several brief remarks regarding the structure of young and perfectly healthy cabbage roots. These show a rather interesting peculiarity in their structure, which, so far as I know, has been considered by no one. Its endodermis or protective sheath[3] is surrounded by a pa-

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[2] M. Cornu: Monographie des Saprolégniées. *Ann. des sc. nat. V. séries*, **15**:120, 137, etc. 1872.—L. Nowakowski: Beiträge zur Kenntniss der Chytridiaceen in die Beiträgen zur Biologie der Pflanzen by F. Cohn. vol. II, part 1, p. 73 and part 2, p. 201.

[3] Schutzscheide (R. Caspary), Gefässbundelscheide, Vaginalschicht, Plerom- oder Strangscheide (J. Sachs), Endodermis (Oudemans, de Bary).—According to de Bary's proposal the generally accepted term "Schutzscheide" should be replaced from now on by Oudeman's prior designation, "Endodermis." (Compare A. de Bary: Vergleichende Anatomie der Vegetations-organe der Phanerogamen und Farne. in *Handbuch der Physiolog. Botanik,* **3**:129. 1877).

renchymatous tissue whose structure reminds one of the so-called secondary or outer protective sheath, present in the roots of several conifers, according to the investigations of Ph. van Tieghem,[4] J. Reinke,[5] E. Strasburger,[6] J. Klein,[7] and others. This peculiarity which until now has been considered as a characteristic feature of only a few conifers[8] is present also in cabbage plants, as is shown by my present investigations.

In the young roots of cabbage plants, each of the most deeply embedded cells of the endodermis immediately adjoining the periblem sheath has a peculiar continuous membranous thickening on its radial and cross walls, as is true of the conifers. This extends into the lumen of the cell in the form of a padded band, and the marvel of it is that the united paddings of all the cells of the periblem sheath always correspond to each other on their inner sides (compare Pl. 31, Fig. 20-23). In a tangential section the thickened rings of each of these periblem cells appear in the form of four-cornered cavities which are packed into the cell and serve to a certain extent as a support. Taken together, these thickenings form a lattice work, that completely surrounds the central cylinder or plerome of the root. It is not unusual, as may be seen in figure 20, to find these peculiar thickenings not only in one but in two contiguous rows of the inner periblem cells, a phenomenon that previously has been observed in several conifers; for example, in *Thuja*.—The characteristic part of the structure of these cells lies in the fact that a very thin and delicate net-like enlargement is present on their inner tangential walls. These nets arise from the above described thickened bands by growing, so to speak, out of these enlargements and extending quite regularly along the inner tangential walls. (Pl. 31, Fig. 22 and 23). So far as the outer tangential walls of these inner periblem cells are concerned, they have at most only a very slight thickening, which does not produce a fully formed net, but

[4] Ph. van Tieghem: Recherches sur la symétrie de structure des plants vasculaires. *Ann. des sc. nat. V. série* **23**:5.

[5] J. Reinke: Morphologische Abhandlungen, Leipzig 1873.

[6] E. Strasburger: Die Coniferen und Gnetaceen, Jena 1872, p. 340.

[7] J. Klein: Zur Anatomie junger Coniferen-Wurzeln, *Flora* 1872, p. 81. Nachtrag, p. 103. Weitere Beiträge zur Anatomie junger Coniferen-Wurzeln. *Flora* 1872, p. 385.

[8] According to the investigations of van Tieghem, E. Strasburger, J. Reinke, and J. Klein, this characteristic is found in the Taxineae and the Cupressineae, but is not present in the Abietineae.

merely the slightest suggestion of one. These enlargements have here the form of very slender simple or branched veins, which also arise from the thickenings already mentioned so repeatedly (Fig. 22). In the young root of the cabbage plant, as in roots of other dicotyledons, the outer parenchyma (the so-called periblem) dies when the plerome begins to enlarge, and gradually is totally sloughed off as far in as the endodermal sheath (Pl. 32, Fig. 24); the inner row of periblem cells that has the above described lattice-like thickening also dies and is sloughed off with the remainder of the periblem sheath.

III

I now take up the description of Plasmodiophora.

If two cross sections are made, the one through a young, perfectly healthy cabbage root (Pl. 32, Fig. 25) and the other through a root of the same age, but already affected somewhat with hernia (Pl. 32, Fig. 26) and the two cross sections are compared, it may be observed that the difference between the two lies in the mere fact that in the diseased root (Fig. 26) several cortical cells are filled with an opaque, hyaline, finely granular, protoplasmic substance, and that the cells immediately surrounding these individuals are slightly enlarged in comparison with the adjoining cells. If a series of cross sections is made of a cabbage root that is slightly more affected (Pl. 32, Fig. 27) and these are examined carefully under a microscope, one soon comes to the conclusion that the gradual enlargement of these hernia swellings is not due altogether to the extreme growth of the individual cells of the cortical element, but also to their great increase in number through cell division. In the largest swellings of the cabbage hernia not only the cells of the cortex but also the vascular element appears abnormally developed or altered. As is shown in the illustration (Pl. 32, Fig. 28), the fibrovascular bundles not infrequently take on an irregularly variable distortion and thereby are shifted from their original normal position. The appearance of such misshapen and distorted fibrovasuclar bundles in the hernia excrescences has already been described by J. Kühn[1] and R. Caspary.[2] In this connection it may be remarked that the

[1] J. Kühn, l.c. p. 253.
[2] R. Caspary, l.c. p. 109.

irregularly distorted vascular ducts in the hernia swellings contain merely air as is true of the ducts in the normal, healthy roots. But so far as the greater part of the cortical cells in the cabbage root protuberances are concerned, some contain, as has been mentioned above, a colorless, finely granular, dense protoplasm, while others are filled completely with minute, globose, colorless bodies. The finely granular protoplasm is the plasmodium and the small globose bodies, the spores of the organism that I have named *Plasmodiophora brassicae*. This organism, which in its structure and development belongs to the Protista (according to the definition of E. Häckel) and is to be considered as one of the very simplest Myxomycetes, penetrates the young, healthy cabbage root, develops there, lives as an obligate parasite, and thereby produces in the tissue the variation and distortion that has already been described.

The plasmodium of Plasmodiophora is constructed like any other plasmodium that might be mentioned. It is composed of a hyaline, transparent, somewhat viscous, amorphous slime substance, in which are embedded colorless, minute granules and oil-droplets. The number and size of the vacuoles in the plasmodium are quite variable, often appearing in whole masses. In the beginning it is almost impossible to differentiate between the plasmodium and the cell contents; it is difficult to say with full assurance which part of the cell has been engulfed by the plasmodium and in which part nothing but the cell protoplasm is still present. Not infrequently the plasmodium appears to be the sole content of the cell that is being studied.[3] At first, the plasmodium is so unusually pale that it is scarcely distinguishable; but, as it develops further and enlarges the host cell, it gradually becomes opaque and takes up more of the entire lumen of the cell (Pl. 32, Fig. 29-34; Pl. 33, Fig. 35, 36). If the plasmodium of Plasmodiophora is to be examined the sections must not be cut too thin, or the water in which the mount is made will rush into the cells containing the plasmodia and will destroy them almost in a moment. It is thus

[3] It is no new idea that the plasmodium can live in the protoplasm of another living organism and develop at its expense. Especially good examples of this are furnished by the Chytridiaceae (e.g. Olpidiopsis, Rozella, Woronina), which have been described by Cornu (l.c. p. 119, 132, 133, 149, 170, 172) as internal parasites of the Saprolegniaceae.

possible to see that the plasmodium is in the form of protoplasmic globules of various sizes, which flow out of the injured cells in the section (Pl. 33, Fig. 37). The globules of the plasmodium, when lying in the water, soon disintegrate by bursting and dissolving. The same phenomenon occurs here as is true in other similar cases, e.g., when the plasmodium of *Aethalium septicum* is dissected or when a vesicle of Vaucheria is injured (compare J. Sachs: *Lehrbuch der Botanik*, IV. Auflage, page 42).

The normal, uninjured plasmodium of Plasmodiophora possesses, in common with all other plasmodia, the power of motion, a movement that manifests itself with the greatest deliberateness. One can make sure of this only by watching the same cell fixedly for a long while. Although it is very difficult to prove absolutely, after further corroborative phenomena one may safely accept the fact that the plasmodium not only moves about in the lumen of one cell but that it oozes from one cell into another. It is very evident that this passing from one cell to another occurs in no other way than through the sieve plates or groups of pits that are present in the walls of all parenchyma cells of the cabbage root (compare Pl. 33, Fig. 40, a, b, and c.[4]) If starch grains are found in the protoplasm of the parenchyma cells of a diseased cabbage root, they are there because they were drawn in together with some of the cell protoplasm by the plasmodium of Plasmodiophora. In other words, it is evident that the plasmodium feeds on these (compare Pl. 33, Figs. 39 and 41). In most cases the plasmodium of Plasmodiophora does not at first entirely fill the lumen of the host cell, but occupies only some definite part. It may lie at one end of the cell (Pl. 32, Fig. 32; Pl. 33, Fig. 39) or form a peripheral girdle, or lie as a cross beam in the middle part (Pl. 33, Figs. 35, 39) or finally, which is much more seldom, it balls up into clumps in the middle of the cell and from this central mass delicate protoplasmic strands radiate out in all directions toward the periphery of the cell (Pl. 33, Fig. 36). After the development of the plasmodium is somewhat more advanced,

[4] According to the latest investigations of C. Cornu, the protoplasm possesses the ability to pass from one cell to another through a living membrane that has neither pores nor pits. (Compare M. Cornu: Sur le cheminement du plasma autravers des membranes vivantes non perforées. *Comptes Rendus* 1877, Premier Semestre, No. 3, p. 133).

it usually takes possession of the whole lumen of the host cell, or at least the greater part of it, and appears at this time to have its whole mass spread out very uniformly. Soon thereafter the whole plasmodium breaks up into spores.

The process of spore formation is similar to that of zoospore formation (compare Pl. 33, Figs. 41-44). The very first step is the arrangement of small globular vacuoles equally distant from each other throughout the whole mass of the plasmodium, dividing it into a fine protoplasmic network or lattice (Pl. 33, Fig. 41). After this a gradual change takes place in the formation. The vacuoles of this network begin to disappear, and simultaneously, the granular substance of the plasmodium lying between the vacuoles collects into small uniform spheroid aggregations. In place of the vacuoles there now appears in the plasmodium an equally large number of small, globose, increasingly well-defined bodies (Pl. 33, Fig. 42, 43). These bodies are the future spores of the Plasmodiophora. They usually fill completely the entire lumen of the host cell and are stuck together as with putty by the colorless water-transparent remnant of the plasmodial slime substance. In this manner the cluster-shaped aggregations of spores usually retain in their contour the size and form of the supporting parenchyma cells.

Special emphasis must be placed here on the fact that no other envelope than the mere cellulose membrane of the containing parenchyma cells surrounds the spores.[5] In all the Myxomycetes (with the single possible exception of Ceratium), even in so simple a form as e.g. Dictyostelium, the spores are surrounded by a mutual covering—a peridial membrane, the structure of which in several forms appears rather complicated. Plasmodiophora has nothing of the kind. The wall of the parenchyma cell in the cabbage plant in which the small, hyaline, globose spores are enclosed replaces here the true sporangial wall. In Plasmodiophora no trace is to be found of a capillitium, which is present in so many Myxomycetes.

In all the parenchyma cells that contain plasmodia of Plasmodiophora, spore formation gradually begins. At

[5] In my previous contribution regarding Plasmodiophora (*Botan. Zeitung* 1875, p. 337) it was stated that in each parenchyma cell a hyaline, transparent, very delicate enveloping membrane was present between the spores and the cell wall. I must retract this statement. It was an error into which I fell easily because my investigations had only just begun at that time.

about the same time the whole group of root swellings begins to decay, a process that is much hastened if the affected cabbage plants are growing in wet soil.[6] If hernia swellings far advanced in decay are examined under the microscope, it is observed that the soft rotting mass is made up almost wholly of free-lying parenchyma cells most of which are completely filled with the aggregations of mature spores (Pl. 33, Fig. 46; Pl. 34, Fig. 47). During the decay the swellings undergo a sort of maceration and disintegration into their several elements. By the still further decomposition due to rot, the walls that confine the spores in the parenchyma cells are reabsorbed and the smeary liquid into which the hernia mass has dissolved is made up almost completely of Plasmodiophora spores, which in part are fully separated and free, while the remainder still lie heaped together (Pl. 34, Fig. 48, 49).

The number of spores is extremely large. The spores are unusually small, their largest measurement not exceeding 1.6μ in diameter. They are perfectly globose and only very rarely are they biscuit-shape (Pl. 34, Fig. 49 and 50). There are double spores, which apparently arise from two spores, that do not separate when they are molded from the plasmodium. The structure of the spore can be observed only by a magnification of 700-900 diameters. They are hyaline with a delicate and perfectly smooth wall, and have a colorless, finely granular protoplasmic content (Pl. 34, Fig. 50, 51).

If the hernia swellings remain long in damp soil they disintegrate completely, thereby liberating the spores in the soil so that the young roots of perfectly healthy plants may become infected by them. The further development of the spores lying free in the soil consists in the swarming of a myxamoeba from each one (compare Pl. 34, Fig. 52). After the myxamoeba has oozed out of the spore and is lying free in the water it possesses a somewhat elongated, spindle-shape body, provided with a rather long, whip-like cilium at its beaked, sharply pointed, anterior end. In the naked protoplasmic body of the myxamoeba there are always present a slowly pulsating vacuole and several small granules, one of these granules usually has larger dimensions than the others.

[6] It has already been stated that the hernia swellings do not decay in dry soil, but under such conditions remain whole, without any apparent change, for a longer or shorter period.

The motility of these myxamoebae is quite characteristic. First, the cilium always is pointed forwards; secondly, the motion is not due exclusively to the cilium but also to the very lively weaving from one side to another of the supple beak; and thirdly, aside from the free movement of the Plasmodiophora myxamoeba as described above, it exhibits still another quite characteristic movement, which resembles creeping or stepping. A delicate thread-like projection stretches out from the lower or posterior end of the protoplasmic body with which the myxamoeba fastens itself to any suitable object lying under the water.

The myxamoeba now contracts this projection and quickly extends another, fixing it to the same object or to some other one lying near by, and so forth; thus without exaggeration it can be said to take real steps (Pl. 34, Fig. 52). The myxamoeba of Plasmodiophora shows also amoeboid movement, as is common to all other myxamoebae (Pl. 34, Fig. 53); but this movement generally occurs later, that is, after the myxamoeba is a few days old.

The myxamoebae of Plasmodiophora force themselves from the soil into the young healthy cabbage roots. Although I was not fortunate enough actually to observe penetration under the microscope, I am convinced of the fact that the myxamoebae enter the cabbage plant through the root hairs and the epidermal cells. I arrived at these (in my opinion) perfectly safe conclusions by the following cultural investigations. I filled flower pots with good, rich garden soil to which I added a given quantity of well-rotted hernia swellings, and sowed fresh seed of various cabbage varieties in these pots. I permitted the young plants produced from these seeds to continue their growth in the pots and watered them daily with water in which fully rotted hernia excrescences had been finely crumbled—water containing a very large quantity of Plasmodiophora spores. Hernia swellings, although as a whole rather small, yet perfectly normal and well developed, appeared on almost every root of the young plants grown in this manner (Pl. 29, Fig. 4, 5; Pl. 30, Fig. 10, 11). On the other hand, no trace of hernia swellings appeared on the roots of cabbage plants grown from the same seed but in soil that was not inoculated with rotting hernia swellings and that were watered with distilled water containing no spores of Plasmodiophora. These roots remained

perfectly healthy throughout the entire experiment. Having the same end in view, still another series of cultures was run through at the same time in the following manner. Young plants were placed in shallow vessels, such as large watch glasses or in porcelain evaporating dishes or on a glass slide, without any soil, but having their roots in water to which had been added a definite quantity of mature spores of Plasmodiophora. I was unable to grow cabbage plants in such water cultures long enough for their roots to show hernia excrescences, but a microscopic examination of the root hairs and epidermal cells of such plants proved very instructive. First, I found these root hairs irregularly swollen in a quite variable manner, even entirely deformed; and secondly, I found in many of them as well as in the epidermal cells an unusually delicate, fully transparent plasmodium, which had exactly the same appearance as does the plasmodium of Plasmodiophora (Pl. 34, Fig. 54 and 55). The experiments here outlined together with my investigations are, so it seems to me, wholly sufficient to assume with absolute correctness that the myxamoebae of Plasmodiophora derived from the soil penetrate the young cabbage roots through the root hairs and the epidermal cells. One may further assume from other experiments of a similar nature that the myxamoebae can force their way into the root and produce infection, not only when it is young, but at a much later stage; that is, the myxamoebae are able to penetrate the roots after these have sloughed off their primary cortical tissue, and are found in the second stage of root development. After they have entered the cells of the root cortex, the myxamoebae of Plasmodiophora mingle with the cell contents, consume it, wander from one cell to another, and thereby produce a violent irritation in all the tissues. The cells suffer an intense hypertrophy and, in the cells of such diseased, much enlarged tissues, there develops from the small microscopic myxamoebae new plasmodia that later are transformed into small globose spores.

From what has been said here of the structure and development of Plasmodiophora, the conclusion may be drawn that it is an extremely simple organism. It is composed merely of a protoplasmic mass—a plasmodium, which, during its whole lifetime, is never enclosed in a membrane

of its own and finally disintegrates into an immense number of small spores, each of which produces a myxamoeba. Each of these myxamoebae enters the tissue of the cabbage root and forms within it a new individual—a new plasmodium. One question that I was unable to answer was whether the plasmodium of Plasmodiophora in the host cell arises from a single myxamoeba or from the fusion of several. This second possibility seems to me by far the more plausible.

Because of the simplicity of its whole structure, *Plasmodiophora brassicae* is a true Protist (according to the definition of Häckel) and therefore stands closest to the Myxomycetes. Cornu (l.c., p. 120) has already pointed out that the Myxomycetes are closely related to the Chytridiaceae; and through Plasmodiophora the affinity stands out still more plainly. Plasmodiophora, in common with the Myxomycetes, possesses a plasmodium that, after a certain time, breaks up into an unbelievably large number of small globular spores that later produce myxamoebae. Plasmodiophora, however, differs sharply from all the other myxomycetal forms in the total absence of a true sporangial membrane and because of its parasitism within another living organism. In every other way, but particularly its manner of living, *Plasmodiophora brassicae* resembles most closely the Chytridiaceae.

IV

Since I have shown conclusively in the foregoing chapter that cabbage hernia is caused by Plasmodiophora, there remains yet the following question to be answered: Is it possible to control this disease? If this is not wholly attainable, is there some means of appreciably lessening the development of Plasmodiophora and thereby reducing the injury to the cabbage plant?

In my opinion the absolute eradication of hernia on the cabbage plant is impossible. It is unthinkable that any substance should kill the plasmodium and spores of Plasmodiophora and at the same time preserve the protoplasm and tissue of the cabbage root in which the Plasmodiophora is parasitic. This substance, whatever it might be and in whatever manner it might be applied, would destroy the cabbage plant when it killed the Plasmodiophora.

The following methods are suggested for definitely checking the development of Plasmodiophora and thereby reducing the injury that the hernia causes on the cabbage plant:

1. The principle method of control and possibly the only real one against hernia is fire. Cabbage stumps usually are left in the field after harvest and by next spring most of them are rotted completely. Later, when the new seed bed is being prepared, the remainder of the cabbage stems and roots are mixed with the soil into which the seedlings are set. This, however, should not be permitted under any consideration. On the other hand, in the fall, or right after the heads are cut off, all the cabbage stems and roots in the vegetable garden should be gathered carefully and burned on the spot. In this manner an appreciable quantity of hernia swellings, in which are a great mass of Plasmodiophora spores, are destroyed in each vegetable garden. The ashes that remain after the stumps are burned can be utilized as fertilizer on other cabbage crops.

2. In the spring, when the plants are set from the seed bed into the field, the strictest and most careful sorting should, by all means, be practiced. Every cabbage plant that shows the slightest trace of hernia should be removed from the vegetable garden and destroyed in no other manner than with fire.

3. Aside from what has been said above, the spread of cabbage hernia can be much reduced if all of the vegetable gardeners use a rational crop rotation in the culture of cabbage. It has long been known and proved by much experience that this practice is of great importance to the grower. Regarding this, compare, for instance, R. Schröder: Russicher Gemüsegarten, Pflanzschule und Obstgarten, Petersburg, 1877, p. 3-4. (In Russian).

R. Schröder[1] gives the advice to the Russian gardeners that in the growing of cabbage they should practice rotation to such an extent that cabbage will not be planted on the same soil oftener than once every two years.

The remedies I have suggested for the control of cabbage hernia are:

1. The burning of the old useless cabbage stumps and their roots.

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[1] R. Schröder is of the opinion that hernia on cabbage plants is caused by the cabbage fly (*Anthomyia*).

2. A strict sorting of cabbage seedlings before they are set into the field.

3. The introduction of a strict, rational crop rotation as a control measure is nothing new within itself, having been introduced among the English and Russian gardeners some time ago, but not enough care was taken in its practice. I am firmly convinced that if these measures are accepted and followed closely there need be no complaint regarding any unusual development and spread of the cabbage hernia.

Still other control measures have been suggested for cabbage hernia, but in my opinion they are not of great importance, and I doubt if their application could be of any real value to the cabbage plants. For instance, in England soot is added to the soil on which cabbage is to be grown and the cabbage plants, before they are set into the field, are dipped in water to which soot has been added. The English, as well as the Germans, remove the hernia swellings by cutting them off with a sharp knife, and find the operation unusually worthwhile, especially when the removing is done while the plant is still young.

The application of guano, saltpeter, salt, bone meal, wood ashes, or other phosphate to the soil can play the rôle only of any other good fertilizer but can not eradicate hernia from the cabbage field.

V

Excrescences that are similar in many ways to the hernia on cabbage are found on many other plants. The real cause for the development of most of these abnormal growths remains almost wholly unknown to us at the present time. The statements that we have regarding them are not at all satisfactory. For example, one may consider as incomplete my work[2] on *Alnus glutinosa* and *Lupinus mutabilis* and that of Eriksson[3] with the legume plants.

I found a parasitic fungus, which I named *Schinzia alni*, in the excrescences on the roots of black alder (*Alnus glutinosa*). J. Eriksson and I found in the root nodules of *Lupinus mutabilis* and of those on *Faba vulgaris* a peculiar

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[2] M. Woronin. Ueber die bei der Schwarzerle (*Alnus glutinosa*) und der gewöhnlichen Garten-Lupine (*Lupinus mutabilis*) auftretenden Wurzelanschwellungen. *Mem. de l'Acad. Imp. des Sciences de St. Petersburg, VII—séries* **10**: No. 6, 13 pp. 1866.

[3] Jakob Eriksson. Studier öfver Leguminosernas Rotknölar. Lund. 1874.

parenchyma tissue, the cells of which were filled with small bodies, and that I probably wrongly took for bacteria or vibrio-like structures. Further research should give us a more intimate knowledge not only of the structure but also of the true cause of the appearance of such root nodules. Similar investigations would most undoubtedly reveal still other new parasites that might be similar to *Plasmodiophora brassicae* or possibly identical with it.

In conclusion, I wish to impart an opinion that possibly might be of value to the animal pathologists. I suspect that the appearance and development of many pathologically abnormal growths and swellings, present on animal organisms, may be explained in the following manner: Small myxamoebae in their various ways gain an entrance into the living organisms where they gradually develop into plasmodia and produce a strong irritation in the tissue of the host organs. This brings about in all the tissues of the organ a pathological change on which the form and size of the diseased growths or swellings are dependent. Further investigations will show whether my supposition can be verified.

EXPLANATION OF ILLUSTRATIONS*

Plate 29

Fig. 1.	Roots of a young cauliflower plant covered with hernia swellings. These plants were taken from the hot bed April 28 to May 10.
Figs. 2 & 3.	Hernia swellings on the common (white) cabbage.
Figs. 4 & 5.	Beginning of hernia swellings on roots of young cabbage plant. (All illustrations on this plate are natural size).

Plate 30

Fig. 6.	Hernia swellings on common (red) cabbage, (a) adventitious leaf buds; natural size.
Figs. 7 & 8.	Swellings on common turnip. Nat. size.
Fig. 9	Hernia root swelling on *Iberis umbellata*, natural size. I obtained this illustration from Mr. O. Wolkenstein.
Fig. 10.	Beginning of hernia on the roots of ordinary (white) cabbage. Nat. size.
Fig. 11.	Commencement of clubbing on the young roots of cabbage seedlings, grown in pots and artificially infected with spores of Plasmodiophora. (a) Nat. size; (b) observed under low magnification of a hand lens.

Plate 31

(Figs. 12, 19, and 20 are magnified 90 times; Fig. 13, 160 times; Figs. 15-18 and Figs. 21-23, 520 times).

Fig. 12-18.	*Chytridium Brassicae*, n. sp.
Figs. 12-14.	Zoosporangia of *Chytridium brassicae* in different stages of their development.
Fig. 15.	Zoospores of *Chyt. brassicae*.
Figs. 16-18.	Resting cells or resting spores of *Chytridium brassicae.*
Fig. 19.	Cross section through a very young, perfectly healthy root of a seedling cabbage plant.
Fig. 20.	Central portion of a cross section through a somewhat older root. In this section is very well shown the characteristic thickening that occurs in the cells of the inner periblem sheath (a S) per. = pericambium (= couche rhizogène of van Tieghem), S. = the endo-

* Translator's Note. These figures are reproduced from those in the original Russian publication. They are here reduced to approximately ⅔ the size of those in the original plates.

dermis (= couche protectrice of van Tieghem, (Schutzscheide of R. Caspary); r, the young side roots growing out from the pericambium.

Fig. 21. A small portion of the above section, much more enlarged, as, S, and per. have the same appearance as in Fig. 20.

Figs. 22a & 22b. Cells of the inner periblem tissue in the tangential longi-section, taken from the inner portion where they are immediately surrounded by endodermis.

Plate 32

(Fig. 27 is magnified 75 times, 24, 25, 26, 28, 90 times; and 29-34, 520 times).

Fig. 24. Cross section through a young healthy root in the stage when the inner parenchyma—the periblem—is already dying and has been sloughed off and the further development is continued in the plerome.

Fig. 25. Cross section through a perfectly healthy root, not affected at all by the disease.

Fig. 26. Cross section through a somewhat older root in which already appear signs of the hernia disease.

Fig. 27. Cross section of a cabbage root, already badly diseased.

Fig. 28. Part of a section through a cabbage root that is still more seriously attacked by the hernia. The bundles present are pushed from their former position and possess various abnormal spiral bands and irregular distortions.

Figs. 29-34. Parenchyma cells, taken from various hernia swellings and containing Plasmodiophora plasmodia. In Fig. 34 the plasmodium contains a few starch grains.

Plate 33

(Figs. 35-39, 40a, 41-43 are enlarged 520 times; Fig. 40b, 712 times; Fig. 45, 90 times; and Fig. 46, 160 times).

Figs. 35 & 36. Parenchyma cells of a diseased root, which contain the plasmodia. In the plasmodium of Fig. 35 some starch grains are found.

Fig. 37. Protoplasmic bodies dissolved in water that occurs when cells containing the plasmodium are cut through with a sharp knife or otherwise injured. In these protoplasmic bodies also lie some starch grains.

Figs. 38 & 39. Parenchyma cells from a clubbed root in which are contained a few further developed plasmodia. In Fig. 39 there are starch grains. Some of these are entirely surrounded by the plasmodium.

Fig. 40. Parenchyma cells of a diseased cabbage root, in the membrane of which are shown sieve-like groups of pits.

Figs. 41, 42 & 43. Plasmodia shown in the act of spore formation. In Fig. 41 are starch grains.

Fig. 44. A semidiagrammatic drawing representing the gradual process of formation in plasmodiophora.

Fig. 45. Cross section through the lamina of the leaf derived from a leaf bud on a clubbed root (Compare with Fig. 6 on Plate 30). As is to be seen here, these leaf buds also are injured somewhat by the disease. Plasmodiophora is already in them and appears in all their further development.

Fig. 46. Free-lying parenchyma cells, appearing as if macerated the most of which contain matured spores. The entire slimy mass consists of such cells and results from the disintegration of the roots having hernia.

Plate 34

(Figs. 47, 48, 49 are magnified 320 times; Fig. 50, 51, 712 times; Figs. 52, 53, 620 times; Fig. 54, 90 times; Fig. 55a, b, and c, 160 times; Fig. 55d, 520 times).

Fig. 47. One of the free-lying parenchyma cells, as in Fig. 46, in which are contained mature Plasmodiophora spores.

Fig. 48. A mass of mature Plasmodiophora spores. The membrane of the host cell is entirely absorbed and the spores, which have been held together in one mass, are about to separate from each other.

Fig. 49. Spores lying free. Two of them double, biscuit-shape.

Fig. 50. Double spores of Plasmodiophora, much enlarged.

Fig. 51. Mature Plasmodiophora spores.

Fig. 52. Spores of Plasmodiophora at the time of myxamoeba formation and the myxamoebae swarming free in the water.

Fig. 53. Myxamoebae of the Plasmodiophora about 6 days after their development from the spores. A pulsating vacuole appears in these myxamoebae.

Fig. 54. Cross section through a young root of a seedling cabbage plant that has been infected artificially with Plasmodiophora spores.

Fig. 55. Root hairs of a cabbage plant, which was grown from seed, on a watch glass in water containing Plasmodiophora spores. In these root hairs are found plasmodia, which are very delicate and almost transparent. 55d is only a portion of 55c with much greater magnification.

PLATES

PLATE 29

Труды С. Петерб. Об. Естествоиспыт. Томъ VIII

Таб. I.

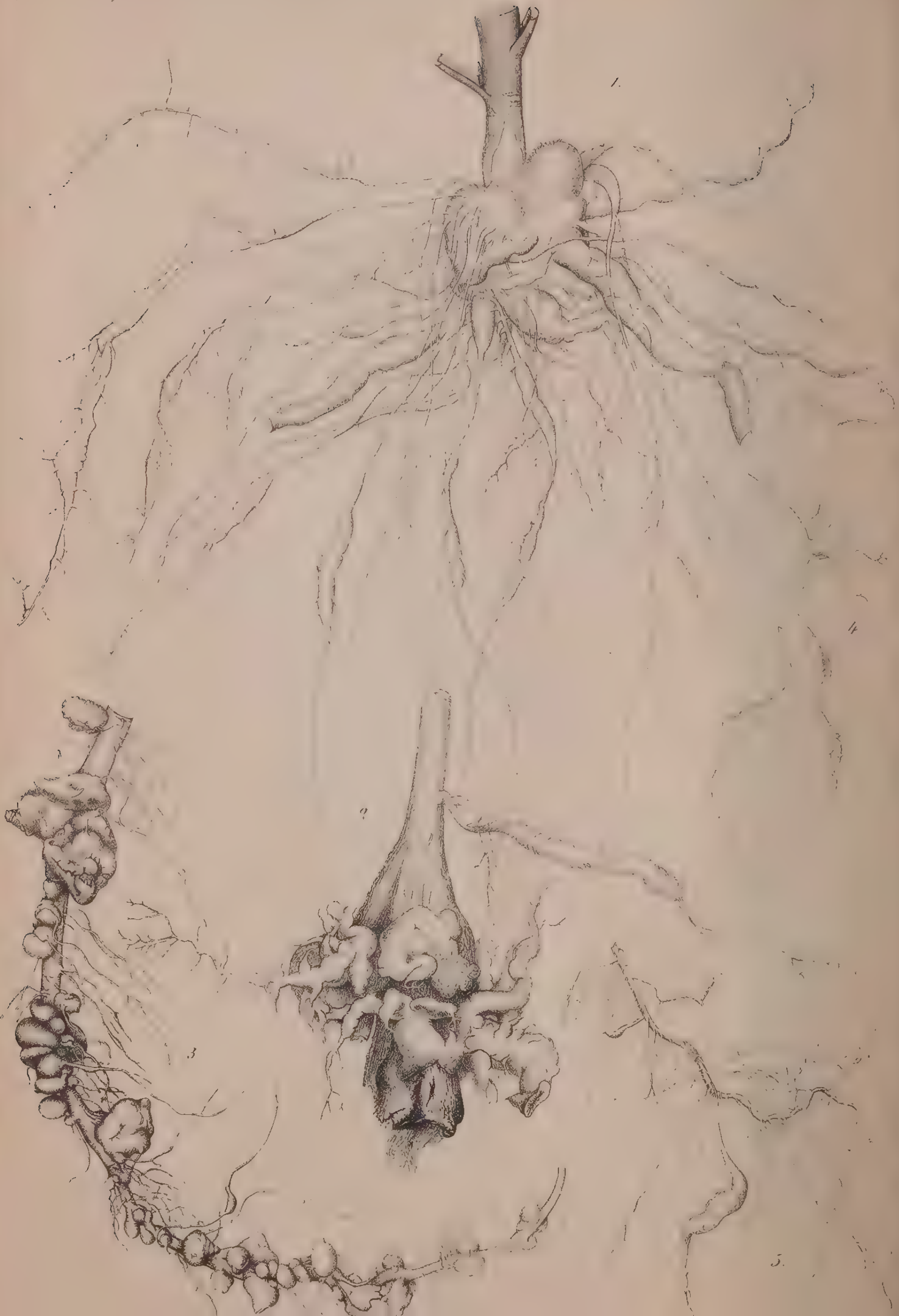
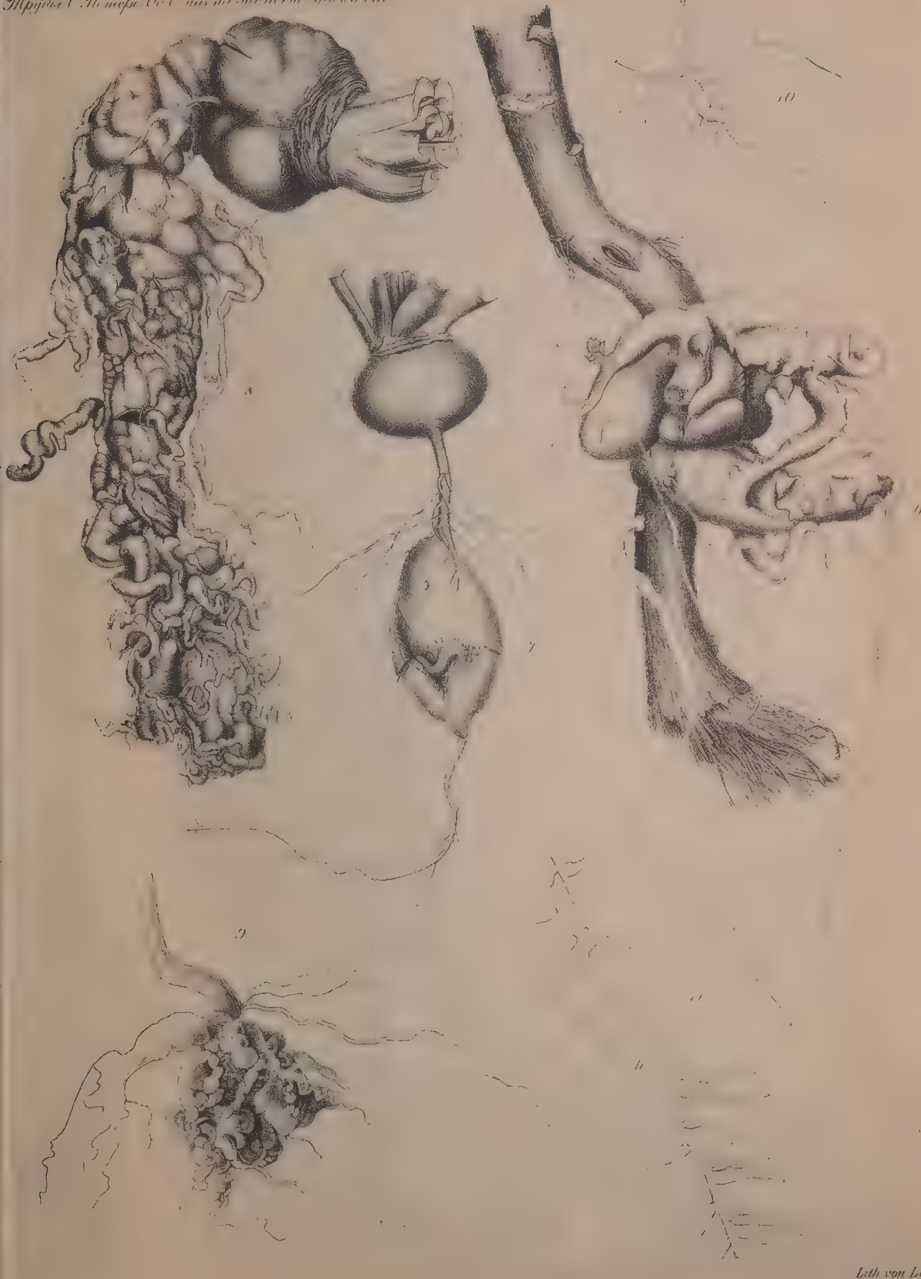


PLATE 30

Труды С. Петерб. Общ. естествоиспыт. Том VIII

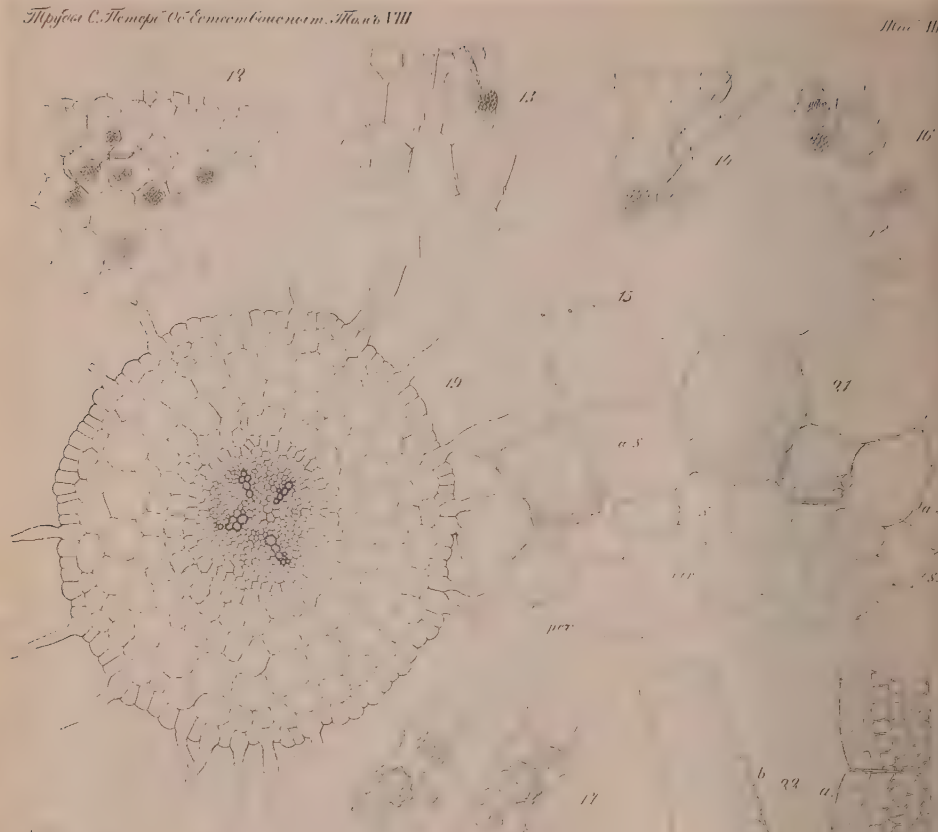
Таб. II.



M. Woronin del.

Lith von Laue.

PLATE 31



Труды С. Петерб. Об. Естествоисп. Томъ VIII
Таб. III
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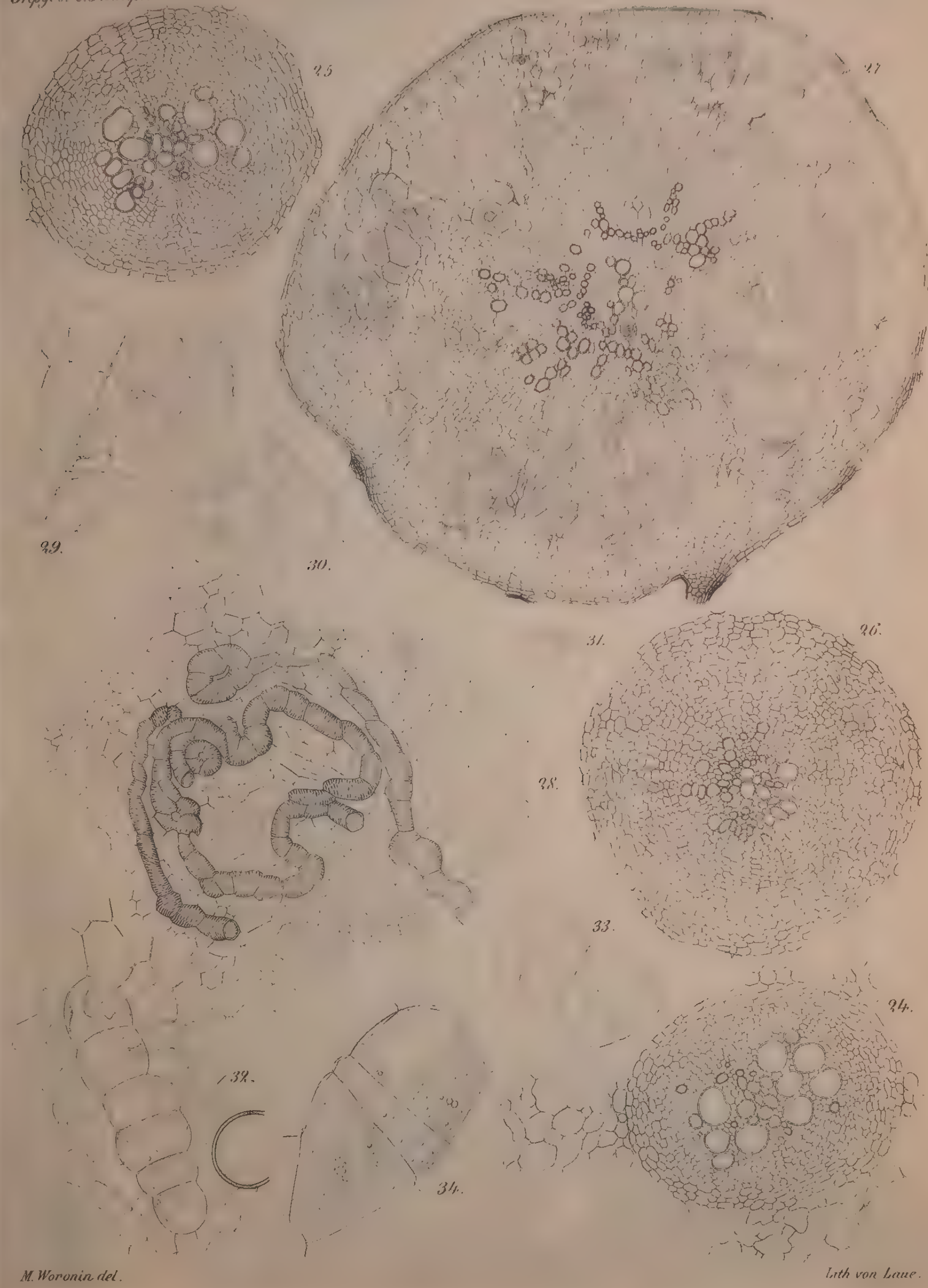
M Woronin del
Lith von Laur

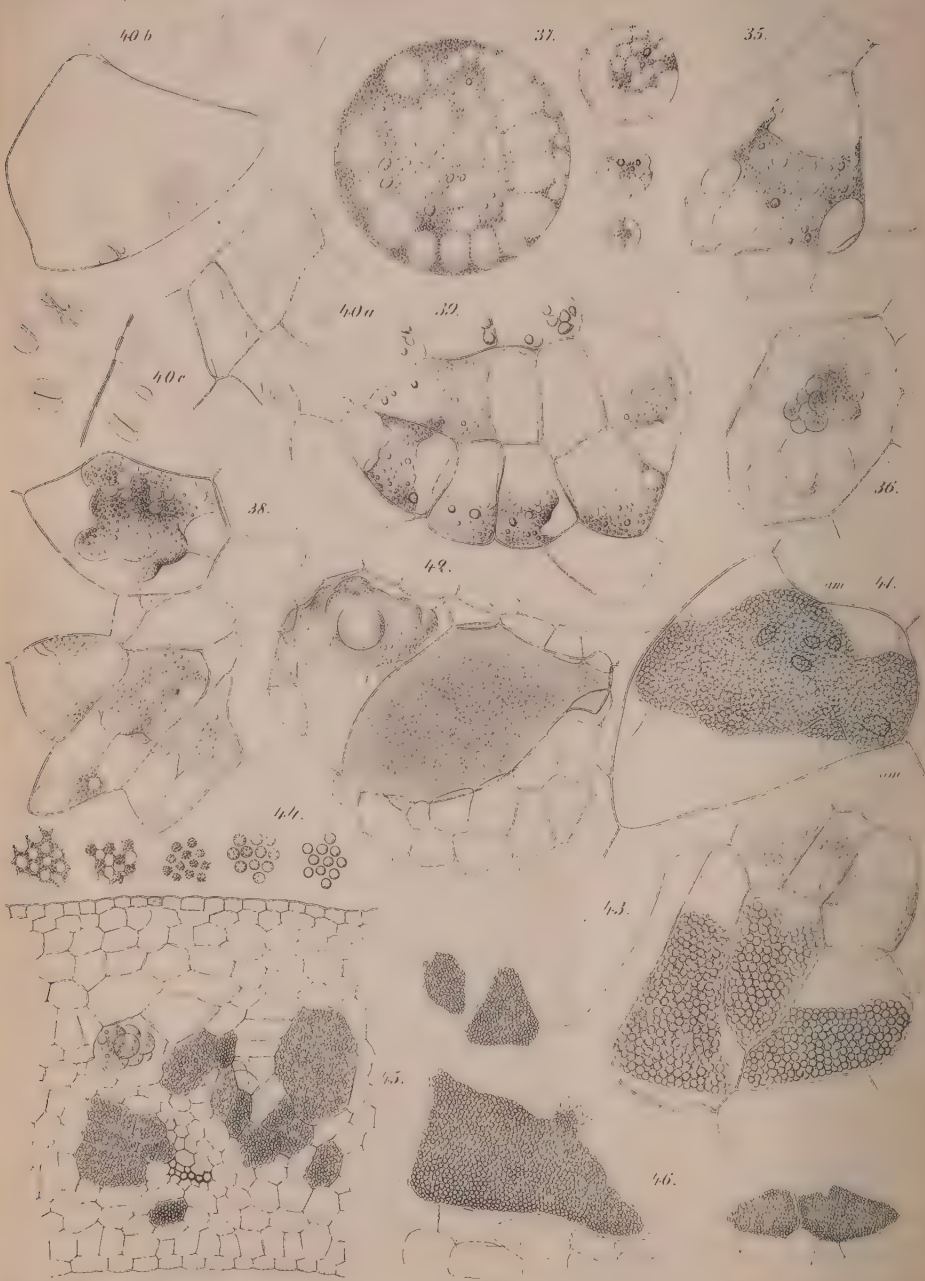
PLATE 32



M. Woronin del.

Lith von Laue.

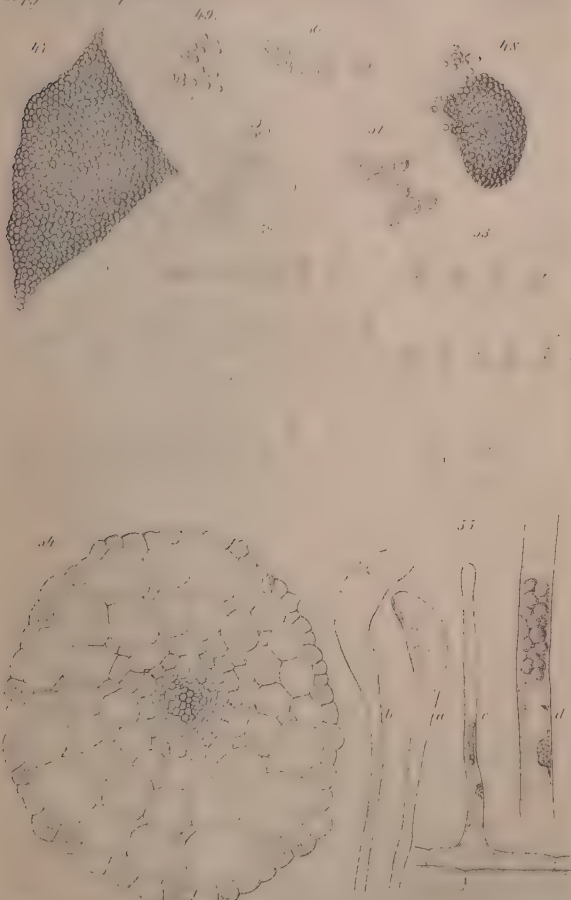
PLATE 33



A. Woronin del. lith. von Laue

PLATE 34

Труды С.Петерб. Об. Естествоиспыт. Томъ VIII. Таб. VI.



M. Woronin del. Lith. von Lane